

The brain is a context machine

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A thesis is presented that the basic operational principle of the brain is to process each input in relation to the context in which it occurs—in space and time. The brain has evolved such that it knows no better or more fundamental approach to computation but contextual comparisons. A brain without context would be a whole another system, with a mind nothing like that of a human.

Key words: context, brain, perception, synchronization

Henri Matisse, a famous French artist said the following about the way he worked: “I don’t paint things. I only paint the difference between things.” Little has he known that, having a human brain, he could not have done much otherwise.

The thesis of the present article is that the default modus operandi of the brain is to process each input in relation to the context in which it occurs. Due to the very principles by which the nervous system is created, it has no other option but base its operations on contextual comparison. These comparisons are embedded so deeply into the function of our brains that without context, our perception would become numb, our ability to think would cease, and our consciousness would turn off.

Inputs to the brain are not represented in their absolute values or categories. Instead, representations of inputs are made exclusively in relation to other inputs—past and present.

These contextual comparisons operate both in time and in space, comparing the inputs either against the past or against other locations. By comparing rather than isolating, the brain works predominantly with discontinuities in the inputs, charging its computational power by the changes and differences in sensory activations.

Receptors and neurons

The contextual nature of brain functioning can be detected already at the level processing of a single receptor cell. A receptor cell transforms the physical input—e.g., light, sound, temperature, mechanical force—into neural signals. While doing so, receptors observe the temporal context. The strength of a response to a given input will depend typically on the strengths of the preceding inputs. If the new input is considerably stronger than the past ones, the response will be vigorous. If this difference is small, so will be the response.

This is explained by the phenomenon of *adaptation*. If a cell is exposed to a constant high-intensity stimulus, the vigor of the response reduces. The cell adapts to the stimulus. The strongest outputs are generated not necessarily by the stimuli of highest absolute amplitudes, but by those imposing largest changes to the previous inputs.

Sensory cells are not the only ones that adapt. Neurons in the central nervous system adapt well too. An orientation

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sensitive cell in the primary visual cortex will respond with high firing rates if a stimulus of a novel, not previously presented orientation is shown. In the same time, this cell will adapt, i.e. reduce the vigor of its response, to a repetitive presentation of one the same stimulus orientation. Among others, adaptation of sensory systems has been reported in vision (Hurley, 2002), audition (Jerger, 1957; Ylikoski & Lehtosalo, 1985), touch (Jones, Gettys, & Touchstone, 1974), and olfaction (Dalton, 2000).

Most dramatic is perhaps the adaptation of the response to a prolonged presentation of a stimulus. At the stimulus onset, a cortical cell will respond with high firing rate. However, as the stimulus remains unchanged, this vigorous response ceases quickly, usually within less than 100 ms—as if the stimulus is interesting for only a short time period and only its change is relevant.

Interestingly, when the stimulus is removed, the cells in the primary visual cortex will respond vigorously again (i.e., off-response), with firing rates often higher than that to the initial appearance to the stimulus (Nikolić, Hausler, Singer, & Maass, 2009). This illustrates the significant extent to which the past context affects the responses to the present stimuli. Apparently, the past tells the brain how much the present matters.

The sensitivity to the context in space is implemented too in the elementary circuits of the brain. In retina, a ganglion cell is inhibited by the activation of other, neighboring ganglion cells—a process mediated through horizontal and amacrine cells (Masland, 2001). This phenomenon is referred to as *lateral inhibition* (Hartline, Wagner, & Ratliff, 1956), and may be the most ubiquitous wiring principle of the nervous system over all sensory modalities. In cortex, lateral inhibition from the regions outside the receptive fields determines the responses to stimuli within the receptive field (Knierim & van Essen, 1992). In the primary visual areas, these mechanisms may affect even the preferred line orientation of a neuron, which depends on the properties of the stimuli presented in the surrounding regions (Silito, Grieve, Jones, Cudeiro, & Davis, 1995).

One important perceptual function achieved through lateral inhibition is our superb capability to detect the edges of the objects in a visual scene (O'Brien, 1958; Shapley & Tolhurst, 1973). Lateral inhibition may play a role in a number of other brain phenomena (Todorović, this issue). Hence, spatial context appears to be as general functioning principle of the brain as is the temporal context.

Vivid illustrations of the above mechanisms are made through perceptual illusions. In vision, popular are the illusions affecting stimulus brightness (Agostini & Galmonte, 2002; White, 1979) or color, illustrating how spatially surrounding areas influence our percepts. Also, visual adaptation is frequently illustrated by after images (see Albright & Stoner, 2002) for a review on contextual influences in visual processing). But less known are the illusions in other modalities. For example, a haptic illusion can be induced by

rotating a piece of chalk between fingers. Due to differential adaptation, a continuous rotating object appears to become thinner in the centre of rotation—obtaining the feel of an hourglass (Jones, et al., 1974). Quickly adapting neurons are responsible also for the feeling of flutter on the skin when stimulated with vibrations (Romo, Hernandez, Zainos, & Salinas, 1998).

In my lab, we discovered that the spatial context does not affect only the firing rates of neurons in the primary visual areas but also their synchronization. Brightness of the stimulus can be induced through contextual changes and can be, in some cases, as we find, explained by the concomitant changes in the synchronization between neurons. A change in the phase between a centre and surround gratings in Figure 1a can affect the perceived contrast of the centre grating. This manipulation of the surround stimulus does not affect

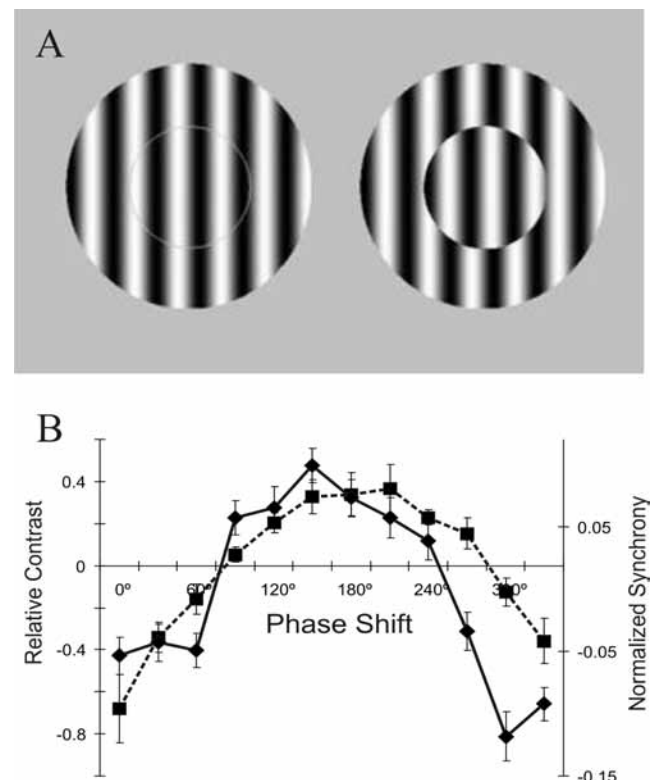


Figure 1. Contextual changes of neuronal synchrony in the phenomenon of brightness induction. (A) The brightness of stimuli on the left and the right are physically identical. The only difference is the relative phase shift of the surround grating. Nevertheless, observers perceive stronger contrast in the centre grating on the right than on the left. This phenomenon is known as brightness induction. (B) Hidden line: Changes in the relative perceived contrast as a function of the phase shift of surround. Solid line: Changes in the strength of synchrony between neurons in cat area 17 whose receptive fields are covered by centre stimuli. Adapted from Biedlack et al. (2006).

the firing rates of cortical neurons responding to the centre grating. Instead, the strength of synchronization between the neurons is adjusted in the brain; The highest perceived contrast is associated with most highly synchronized discharges of cortical neurons (Figure 1b; Biedlack, et al., 2006).

Adaptation and lateral inhibition are not the only brain mechanisms sensitive to context. Also, not all contextual influences take place at low levels of processing (Vladusich, Lucassen, & Cornelissen, 2006). Others mechanisms exist, and some operate also at higher levels of system complexity. For example, those based on processing shades of gray (Agostini & Galmonte, 2002) are entirely context dependent, and are physiologically poorly understood. Also, the simplest form of visual memory, sensory storage (aka iconic memory), does not store information about an image independently of a previous one. Instead, sequentially presented images interact in a non-linear way in neuronal responses (Nikolić, et al., 2009) to produce perceptual effects of competition and integration (Di Lollo, 1977, 1980)—which is a process that relies on mechanisms other than adaptation (Nikolić, et al., 2009).

In general, it appears that the basic circuitry of the brain is utterly incapable of maintaining the absolute information about the physical world (e.g., temperature, mechanical force, light intensity, etc...). Instead, the brain has no other source of information but that presented relative to the context in which it emerged. Evidently, when a big brain gets wired, the result a massive context machine.

The system in global action

If the building blocks of the brain obey context, the same may be expected from the entire system when fully integrated with all its functions. Consciousness is of interest here, a phenomenon that embodies, arguably, a high level of the organization of a nervous system.

Studies have shown that the dynamics of consciousness is heavily affected by the context. Similarly to the adaptation of sensory cells, the contents of consciousness—i.e. the pieces of information that attempt to, or succeed receiving the focus of attention—depend on the history. Simply put, our brain prefers novelty. We are more likely to pay attention to novel than to familiar stimuli. This preference for new, which is a next of kin to adaptation, has been demonstrated empirically most clearly in the phenomenon known as *inhibition of return* (Klein, 2000; Posner & Cohen, 1984).

In the spatial domain, the novel and unusual drives attention and directs consciousness equally well. Most extensively studied are the discontinuities in a visual field—i.e. unique sets of features, different from the remaining parts—, which induce perceptual pop-out, attract attention, and possibly give rise to the subjective experience of visual awareness. Conditions that lead to perceptual pop-out can be studied in experiments with serial visual search (A. Treisman, 1982; A. M. Treisman & Gelade, 1980)(see Figure 2).

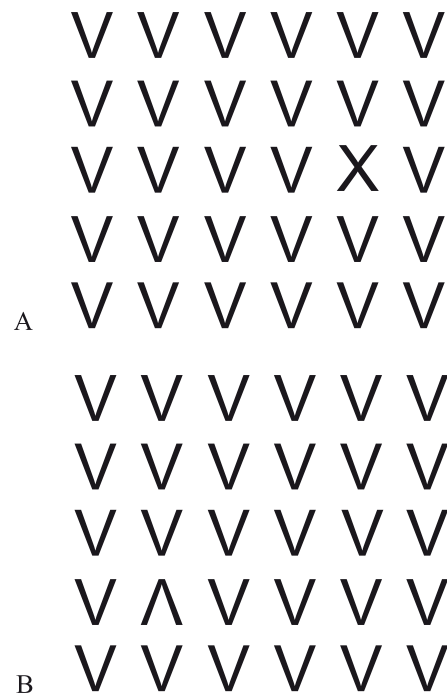


Figure 2. Examples of stimuli used in serial visual search tasks. An X, among V's is much easier to detect (A) than an inverted V (located in lower-left corner in B) among V's. Such experiments lead to the proposal of feature binding theory and to understanding the conditions under which the discontinuities in the visual field can lead to perceptual pop-out—i.e., to context-dependent processes that attract attention involuntarily and automatically to the novelties and irregularities in the visual field.

Thus, the unusual and the new seem to account for a big part of what we perceive, process and memorize—locally and globally. Context is hence, a fundamental operating principle at all system levels. Our mind does not simply treat the input verbatim. Instead, the mind is “biased” by the past and by the neighboring regions. Context matters.

Where do then absolute categories come from?

A question then arises of absolute categories, which our brains can also work with. An absolute perception of stimulus intensity requires effort (Robilotto & Zaidi, 2004) but cognitive operations seem to work with constancies at least as well as with relations. For example, although Mark can be tall or short, depending on the context—short when compared to basketball player Magic but tall when compared to gymnast Merry—Mark measures always 175 cm from head to toe irrespectively in whose company.

Our brains can obviously think in terms of meters, and thus in absolute categories for expressing the length of an object. How does a contextual hardware produce these ab-

solute representations, which operate for example in working-memory (Brody, Romo, & Kepecs, 2003)? And do these aptitudes suggest principles of brain function other than contextual?

I think that the answers are in the ability of the brain to *conceptualize*, i.e., to categorize the world. Categorization is an important component of perception—e.g., Does a particular sound represent a predator or a prey?—and even more important for thinking. The ability to categorize is considered a high-level function. The regions of the brain responsible for the representation of concepts, located in inferior and superior temporal cortex (Mummary, et al., 1999; Nobre, Allison, & McCarthy, 1994; Zahn, et al., 2007), lay at high levels of the information processing hierarchy. Absolute categorization of length in meters is a form of categorization.

Importantly for the present discussion, conceptualization in absolute categories does not seem a hallmark of the basic circuitry of the brain. Instead, such functions have likely evolved, through evolution, on top of other mechanisms that, originally, were not able to categorize. The contextual brain has to go through a great deal of effort to establish an absolute category. Not all forms of nervous systems may be equally capable of doing so. Unlike the automatic, effortless and unavoidable detection of edges, formation of such advanced forms of concepts is hard work.

Absolute categorization may require involvement of functions located at a level of processing even higher than concepts, those responsible for implementing *logic*—a capability of clear thinking executed by hardware of fuzzy computing. At present, we do not know how this implementation happens. The mechanism responsible for logic and conceptualization are unknown.

It would be a mistake to assume that the basic building blocks of the brain and thought obey the rules of logic. This mistake has been already made once when the research field of *artificial intelligence* has made a promise to bring von Neumann computers to the level of human intelligence—as it was assumed that that we think like computers and computers think like us (Newell, Shaw, & Simon, 1958). The promise failed downright (Lighthill, 1973). Computers cannot think or perceive like humans do. Cognitive neuroscientists should not repeat that mistake. The evidence accumulated meanwhile indicating that the hardware of the brain is a fuzzy, context-dependent system. Throughout the evolution, clear conceptual thinking is created only later and is built, in an unknown way, upon these rather blurry basics. In our heads, the shiny logical software works on mucky contextual hardware.

Why context?

I assert that the reason for the brain circuits being, by their nature, contextual is an evolutionary accident, perhaps

serendipity. There is no great wisdom or plan in forces that drive evolution of organisms and their brains. Evolution “works” with whatever it has at hand. It builds on top of the existing. And so does the evolved brain. Hence, in an early stage of pre-nervous-system evolution, it may have happened so that cells implemented simple regulatory reflexes but had to adapt to inputs for some simple reason such as the quick depletion of resources. Then, in the next stage of evolution, when a bit more complex circuits were “implemented”, no alternative existed but to integrate this adaptation of the cells as a part of whatever new design has been created. This way, the initial random choice of a regulatory mechanism kept being carried on through further evolutionary steps to ever more complex designs of the nervous systems—all the way to *Homo sapiens*. An initial disadvantage became a computational principle. A bug became a feature.

The implementation of consciousness, especially the component of its subjective experiences (i.e. the qualia), is a mystery to modern neuroscience. These phenomena seem unexplainable. My hunch is that the problem lays in our theories being inspired too strongly by computer technologies. Consciousness may be much less of a theoretical problem if the brain theories, e.g. those of vision, immerse considerably deeper into contextual considerations of the perceptual principles than is the case today. By doing so, the discipline should abandon computer metaphors.

A good example is feature detection. Today’s theories assume that neurons in early visual cortex detect elementary features of the presented visual objects (Hubel & Wiesel, 1962). The problem is that feature detection is a tribute to an absolute category; Features are supposed to belong to objects independently of the surroundings.

The function of a neuron in V1 may be a bit different than assumed by the feature-detection theory. As theorists, we may do better if, instead, we consider orientation selectivity of a cortical neuron as responding to contextual (ir)regularities in the visual field, leaving the perceptual processes associated with elementary visual features to higher brain areas—possibly to the interaction between those involved in categorization, such as the temporal lobe (Mummary, et al., 1999; Nobre, et al., 1994; Zahn, et al., 2007) and those guiding our attention, such as the parietal lobe (Colby & Goldberg, 1999; Farah, Wong, Monheit, & Morrow, 1989). This may relief the explanatory burden imposed on the early processing stages by the perception theories and may, in the same time, open explanatory doors for understanding the mechanics of subjective visual experiences—i.e., the qualia. Such fundamental changes in theoretical principles may be slow and painful, but may also pay off.

Possibly, the brain computations, unlike our theories of those computations, are so deeply dependent on the context that, without it, no candle of awareness can light up. The brain may be actively engaging mechanisms to seek or

induce changes and novelty, especially in the environment that is poor in delivering such changes on its own. The eye movements during a fixation may be an example of such an active quest for change. Our eyes, when healthy, make micro-movement with a frequency of 30–100 Hz and of miniature amplitude, which seem to play an essential function in enabling visual perception. If these movements are abolished (actually their effects are abolished through innovative optic devices), our perception of the world fades away (Martinez-Conde, Macknik, & Hubel, 2004). If the surrounding world does not change, the brain makes it change. A constancy of the input seems to bring the perceptual fire to a still. The dynamics of change seems to keep marry-go-round.

By all means, this conclusion extends to phenomena other than adaptation of sensory inputs. Without the sensitivity to changes in time and space, we may not only reduce the contents of our awareness; The awareness may completely switch off.

Static representations and absolute values of the surroundings may be, in principle, also possible to implement by biological systems. But apparently, such mechanisms would be the workings of some other brains, not those evolved on the planet earth. Perhaps, these static brains would produce minds of “dry” thought and “dark” perception, uncharacteristic of human brain—but perhaps attributable to the artificial silicon ones sitting on the tables in our offices.

In visual arts, if the outlines of an object—i.e., the lines of demarcation—are put on the paper or canvas, our brain has enough to work with to perceive meaningful objects. Henri Matisse, being human, had the perceptual apparatus tuned for detecting and working with differences between objects, and so did the audience who appreciated his creations. Whatever feature or detail of a scene the master wanted to emphasize, whatever visual message he wanted to convey, excerpting the distinction between the aspect of interest and everything else in the image was probably the best, if not the only way to create and enjoy a piece of art.

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